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# Paleogene Origin Of Planktivory In The Batoidea

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RH: UNDERWOOD ET AL.—ORIGIN OF PLANKTIVOROUS BATOIDS

ABSTRACT—The planktivorous mobulid rays are a sister group to, and descended from, rhinopterid and myliobatid rays which possess a dentition showing adaptations consistent with a specialized durophagous diet. Within the Paleocene and Eocene there are several taxa which display dentitions apparently transitional between these extreme trophic modality, in particular the genus *Burnhamia*. The holotype of *Burnhamia daviesi* was studied through X-ray computed tomography (CT) scanning. Digital renderings of this incomplete but articulated jaw and dentition revealed previously unrecognized characters regarding the jaw cartilages and teeth. In addition, the genus *Sulcidens* gen. nov. is erected for articulated dentitions from the Paleocene previously assigned to *Myliobatis*. Phylogenetic analyses confirm *Burnhamia* as a [sister taxon to the mobulids](#), and the Mobulidae as a sister group to *Rhinoptera*. Shared dental characters between *Burnhamia* and *Sulcidens* likely represent independent origins of planktivory within the rhinopterid – myliobatid clade. The transition from highly-specialized durophagous feeding morphologies to the morphology of planktivores is perplexing, but was facilitated by a pelagic swimming mode in these rays and we propose through subsequent transition from either meiofauna-feeding or pelagic fish-feeding to pelagic planktivory.

## INTRODUCTION

Microphagous planktivores are important elements within modern oceanic ecosystems. Despite this, planktivory has evolved [relatively few times within](#) vertebrates. Of the clades of extant planktivorous chondrichthyans, three are monospecific (the whale shark *Rhincodon typus*, basking shark *Cetorhinus maximus*,

and megamouth shark *Megachasma pelagios*) and one, the Mobulidae (devil rays and mantas), is composed of multiple species within two genera. All of the planktivorous chondrichthyan clades have a long fossil record—extending to the Late Eocene (about 35Ma) or earlier. In addition, there are several problematic fossil genera (including *Archaeomanta* and *Cretamanta*) that appear to represent extinct planktivorous clades (e.g. Enault et al., 2013). In contrast, only a single clade of large planktivorous actinopterygian fish is known from the fossil record, and that was restricted to the Mesozoic (e.g. Friedman et al., 2010; [Friedman 2012](#)).

The extant mobulid rays comprise two genera of medium to very large batoids that are present in all tropical and subtropical seas. They possess adaptations for a pelagic lifestyle, such as oscillatory swimming (Schaeffer and Summers, 2005) and have cranial, brachial, and oral adaptations for microphagy (e.g. Paig-Tran and Summers, 2014). The Mobulidae share a clade with the Myliobatidae and Rhinopteridae (e.g. Aschliman, 2014 and refs therein); two families with numerous specialisations for extreme durophagy, including an extremely robust dentition (e.g. Underwood et al., 2015), modified tooth histology (Herman et al., 2000), and jaw cartilages strengthened with internal trabeculae (Summers et al., 1998). It therefore appears as if the evolution of mobulids has been associated with a shift between two very specialized, and very dissimilar, trophic styles.

The Paleogene genera *Sulcidens* gen. nov. and *Burnhamia* Cappetta, 1976 appear to show dentitions transitional between that of durophagous taxa and extant planktivorous mobulids. A number of other genera demonstrate progressive change from the tooth morphology possessed by *Burnhamia* and the progression towards the morphologies possessed by extant species of *Mobula* and *Manta* (Adnet et al., 2012).

## MATERIALS AND METHODS

The holotype of *Burnhamia daviesi* (Woodward 1889) is preserved within a concretion from the London Clay, (Eocene, Ypresian) of Sheppey, S.E. England. The exact collection site is unknown but it was probably collected loose on the beach between Warden Point and Minster on Sea. Comparative material [studied here was collected loose from the same area over a period of several decades by DJW](#).

Specimens of *Sulcidens sulcidens* (Darteville and Casier, 1943), *Sulcidens* Sp. and “*Myliobatis*” *raouxi* Arambourg, 1952 were obtained from the phosphorites of the Oued Zem area, northern Morocco. [The figured material was recovered from commercial sources near Oued Zem, and represents material collected locally by mine workers. The exact provenance of the material is uncertain. The matrix lithology or fine, white to pale tan, phosphatic oolite is consistent with the local Paleocene \(CJU and DJW pers. obs\). In contrast, Maastrichtian matrix is largely yellow and biodetrital, with Ypresian matrix being pale grey to buff and peloidal. In addition, associated fossils in the same batches included \*Palaeocarcharodon\* and other taxa otherwise recovered from Paleocene levels \(CJU and DJW pers. obs\). The Paleocene levels are poorly dated and multiple distinct faunal assemblages are present. The stratigraphic interpretation of these is beyond the scope of this study.](#)

The holotype specimen of *Burnhamia daviesi* was scanned at the NHMUK using the Metris X-Tek HMX ST 225 CT system. Scan data was rendered in VG Studio MAX. [Segmentation of elements of the fossil proved unreliable due to](#) the fragmented nature of parts of the mineralized cartilage and the irregular presence of X-ray dense pyrite. For that reason, some images are composites of several scan renderings,

merged in Adobe Photoshop, with Photoshop also being used to highlight areas of interest.

For phylogenetic analyses, we used genera as our operative taxonomic unit (OTU) for all analyses, outside the Myliobatidae, Rhinopteridae and Mobulidae. Our data matrix consists of 34 jaw and dental characteristics for 26 OTUs, as well as 43 [additional](#) morphological characters from Claeson et al., (2010). Seven of these taxa are in-group myliobatids (Rhinopterines, Mobulines, Myliobatines, and Aetobatines), with *Raja* and *Rhinobatos* rooted as our nominal outgroups to all myliobatiforms (stingrays). The most-inclusive molecular study (Aschliman et al., 2012) place skates (Rajidae) as sister to all other batoids, with a paraphyletic assemblage of guitarfishes as sister to remaining myliobatiforms and allies (Hexatrygonidae, Zanobatidae, Plesiobatidae). Fourteen characters were modified from Claeson et al. (2010), with only two characters (presence/absence of lower jaw “wing processes;” fusion of the medial jaw symphyses) regarding the condition of the jaws taken from other sources (Carvalho et al., 2004; Lovejoy, 1996 and Claeson et al., 2010, respectively).

Surprisingly few jaw characters have been used as traits for systematic study, with this study generating thirteen characters for describing jaw shape. All characters were treated as unordered and equally-weighted. These traits are described in the supplementary material. Characters were scored as missing data (?) when the condition is unknown or variable within a genus (traits not able to be determined from preserved specimens or computed tomography scans). Character states were scored as non-applicable (-) in cases where the character was absent as a homologous structure in particular OTUs. The data matrix was analyzed using PAUP\* 4.0b10 (Swofford, 2002) using the maximum parsimony optimality criterion. We employed heuristic searches with 1000 replicates of random stepwise addition using TBR (tree-bisection-

reconnection) branch swapping. The “amb-” option was used to collapse soft polytomies if branch lengths were equal to zero. All figured specimens of fossils are deposited in the Natural History Museum, London (NHMUK).

## SYSTEMATIC PALEONTOLOGY

NEOSELACHII Compagno, 1977

BATOIDEA Compagno, 1973

MYLIOBATIFORMES Compagno, 1973

MOBULIDAE (s.l.) Whitley, 1936

*BURNHAMIA* Cappetta, 1976

(Figs 1–3)

**Type Species**—*Rhinoptera daviesi* Woodward, 1889

**Amended Diagnosis**—Jaw cartilages robust. Palatoquadrates not fused at symphysis and rhombic in cross section near symphysis, with inner surface becoming concave laterally. Constriction in cartilage lateral to the teeth, with a posterolateral flange projecting from the upper part of the cartilage. Meckel’s cartilage strongly expanded anteroposteriorly; flattened with convex outer and concave inner surfaces. Laterally projecting flange present on lower surface from a point lateral of the outermost teeth. Internal trabeculae present but poorly defined.

*BURNHAMIA DAVIESI* (Woodward, 1889)

(Figs 1–3)

*Rhinoptera daviesi* Woodward, 1889: III, 6 (original description).

*Rhinoptera daviesi* Woodward, 1889: Woodward, 1899: 5.

*Rhinoptera daviesi* Woodward, 1889: Leriche 1905: Figs 10-12.

*Rhinoptera daviesi* Woodward, 1889: Leriche 1906: Figs 34-36.

*Rhinoptera daviesi* Woodward, 1889: Leriche 1922: 8, 3-5.

*Rhinoptera daviesi* Woodward, 1889: Davis 1936: 334.

*Rhinoptera daviesi* Woodward, 1889: Casier 1946: 3, 7a-f.

*Rhinoptera daviesi* Woodward, 1889: Casier 1947: 4, 4; Fig. 7.

*Rhinoptera daviesi* Woodward, 1889: Casier and Stinton, 1966: 9, 8-9.

**Holotype**—NHMUK P.1514, comprising the largely articulated left side of the jaws within a phosphatic concretion

**Amended Diagnosis**—As above and see Woodward (1889).

**Material**—The holotype, NHMUK P.1514. In addition, isolated teeth, also collected loose from Sheppey, were studied for comparative purposes (Fig. 3).

## DESCRIPTION

**Jaw Cartilages**—The specimen preserves all but the lateral extremities of a left palatoquadrate and a near complete Meckel's Cartilage missing the lateral extremities and the symphyseal region (Fig. 1A, B). Parts of both jaw cartilages are visible on the specimen surface, but their form is only revealed in renders of CT scans (Fig. 2A–D).

The Palatoquadrate is robust and somewhat arcuate. It is about 3 times as wide (from symphysis to jaw joint) as anteroposteriorly deep. At the symphysis, the cartilage is anteroposteriorly expanded, being deeper than high. At this point the



cartilage is rhombic in section and the upper surface inclined to the posterior (Fig. 2D). Away from this point, the lingual (inner) surface becomes progressively more concave. The labial (anterior) edge of the cartilage is straight in the central region where teeth are present, lateral to which it is smoothly concave until the jaw joint. Adjacent to the point where the concavity in the anterior jaw margin starts, the upper surface of the cartilage is expanded to form a flange that is directed latero-posteriorly, overhanging a rather flatter lateral part of the cartilage. The indented surface for the jaw hinge is expanded anteroposteriorly, but is laterally compressed. Irregular trabeculae are present (Fig. 2 E, F). It is uncertain to what degree taphonomic processes have destroyed the trabeculae, but they are widely spaced and rather irregular. Some trabeculae are seen to traverse the thickness of the cartilage, others appear to extend from the outer face but not reach the inner face.

The Meckel's cartilage is strongly anterolaterally expanded. The lingual (inner) face is somewhat concave but poorly mineralized and details are not clear. The linguo-basal (lower) surface is gently convex meeting the inner face posteriorly at a sharp angle. The lateral part of the lower face of the cartilage is considerably more compressed than in the central part of the jaw. There is a sharp boundary between the more and less compressed parts of the cartilage, with a lateral concavity behind a small flange that extends laterally from the central part of the jaw. The hinge area is incompletely preserved, but a deep articular surface is present and the lateral-most part of the cartilage is seen to be reflexed upwards. There was no evidence for preserved trabeculae.

**Dentition**—The left side of the lower dentition is preserved largely in articulation (Fig. 1C, D; Fig. 2A, C), whereas upper teeth are present scattered both around the jaw margin and within the interior of the mouth (Fig. 2A, B, D). Although preserved

in near articulation, the teeth are not closely locking and adjacent articulated teeth are only loosely in contact.

The lower dentition (Fig. 2A, B; green) comprises a symphyseal tooth file (only partly preserved) and five alternating lateral tooth files. Whilst the width of the symphyseal teeth is uncertain, other tooth files show a progressive narrowing of the teeth away from the symphysis. The narrowing of the teeth is associated with a decrease in the number of root lobes, with nine root lobes being present in parasymphyseal teeth to only three in the teeth closest to the commissure.

The upper dentition is seen only as disarticulated teeth (Fig. 2A, B; purple). These are similar in overall size to the lower teeth, but more compressed linguolabially. A partial probable symphyseal tooth has 11 root lobes preserved and was presumably wider originally. Other teeth appear to have a rather bimodal size distribution, with many having seven to nine root lobes or two to three root lobes, with few of intermediate size. This suggests a more disjunct heterodonty than that seen in the lower dentition.

The details of tooth morphology could be more readily observed on isolated teeth than the holotype specimen (Fig. 3). Many of the isolated teeth are rather larger than the teeth of the holotype; whilst this may be largely due to collection bias towards larger specimens, it may also suggest that the holotype represents a small or juvenile individual. All teeth are the same height, or generally lower than (linguolabially) deep, and all but the smallest teeth have two root lobes, seen to be upper lateral teeth in the holotype, which are wider than deep. Lingual and labial faces of the teeth are straight or, in larger teeth, have a faint sigmoidal curvature. The lateral ends of the tooth (in occlusal view) are sharply angled and triangular, with an internal angle of

between 90 and 120 degrees. The narrowest teeth (with two root lobes) are approximately hexagonal in occlusal view.

The root is low, comprising approximately half the height of the tooth, slightly smaller (in basal view) than the crown and slightly offset and inclined lingually. Between two and 17 root lobes are present although the larger teeth are commonly broken and so larger counts of root lobes may be present in some teeth. In most teeth all root lobes are similar size, although one or more narrower root lobes may be present. The tooth with 17 root lobes (Fig. 3A–C) has a sigmoidal occlusal profile and is therefore probably not a symphyseal tooth. Root lobes are widely spaced, with the gap between root lobes being at least as wide as the root lobes, and have a rounded basal face. Irregular foramina are present between the root lobes.

The tooth crown lacks true cusps and is the same height across the width of the tooth. It has a covering of enameloid that is not removed by in-life wear. It overhangs the top of the root labially and laterally. The lingual, labial and lateral faces of the crown are somewhat concave and covered in fine, but well developed, granulations. The occlusal face of the crown is concave along the whole width of the tooth. This is completely covered by fine granulations, smaller and less defined than those on the sides of the crown. The edges where the occlusal and other faces of the crown meet are sharp and slightly irregularly crenulated. In a small number of teeth (not seen in the holotype) there may be an irregular, corrugated ridge or ‘wall’ around the edge of the occlusal face, which is slightly lingually inclined (see Fig. 3J–O).

## DISCUSSION

The jaw cartilages are very robust overall, a character seen in strongly durophagous taxa such as members of the Myliobatidae (e.g. Fig. 4C) and Rhinopteridae as well as disparate batoid taxa such as *Rhina*, *Pastinachus*, and *Narcine*. The general shape of the jaw cartilages are similar to those of the Myliobatidae and Rhinopteridae, but differ from both in detail. In particular, the lack of fusion of the palatoquadrates differs from the situation in the Myliobatidae, Rhinopteridae and Mobulidae, where there is complete fusion of left and right jaw cartilages. Likewise, the rhombic cross section of the palatoquadrates differs from the flat-topped, semicircular cross section in the Myliobatidae and Rhinopteridae and the extremely compressed shape of the Mobulidae. The oval cross section of the Meckel's cartilages also differs from the form seen in Myliobatidae and Rhinopteridae (see Fig. 4) and is more reminiscent of the form seen in the Mobulidae. The presence of trabeculae unites *Burnhamia daviesi* with the Myliobatidae and Rhinopteridae, as well as possibly the Mobulidae, although trabeculae are also present in unrelated taxa such as *Rhina* (CJU pers obs) and *Narcine* (Dean et al., 2006).

Wide teeth with multiple root lobes are restricted to the Myliobatidae, Rhinopteridae and some of the Mobulidae, in addition to *Brachyrhizodus* and *Igdabatis*; Late Cretaceous taxa of uncertain affinities (see Cappetta, 2012). All extant members of the Myliobatidae have highly disjunct heterodonty with a very large symphyseal tooth and, where present, very reduced lateral teeth. In the monogeneric Rhinopteridae there is a gradient heterodonty, with the largest teeth at the symphysis and the smallest lateral to that, although it should be noted that there is considerable variations between individuals of some species. All extant Mobulidae have large numbers of very small teeth and are typically homodont (e.g. Adnet et al., 2012). The adjacent teeth of myliobatids are tightly locked together, with complete dentitions

commonly remaining articulated after death, unlike the dentitions of the Rhinopteridae and Mobulidae. The overall pattern of the dentition of *Burnhamia daviesi* is therefore most similar to that of the Rhinopteridae, although the upper dentition appears to have been somewhat reminiscent of *Myliobatis*. Despite this, teeth of the Rhinopteridae have a high crown and robust roots, and fit tightly together within the dentition. The crown of the Rhinopteridae exhibits strong in-life wear and the thin enameloid layer is removed to expose the dentine layer which is packed with vertical tubules, a situation also seen in the Myliobatidae, with which they share a complex enameloid structure (Enault et al., 2013). Teeth of modern Mobulidae, in contrast, are delicately constructed and show little or no in-life wear (see Adnet et al., 2012). The teeth of *Burnhamia daviesi* therefore share characters with the Mobulidae. In addition, the dental histology of *Burnhamia*, although somewhat unclear, is far more like that of the Mobulidae than Myliobatidae or Rhinopteridae (Enault et al., 2013).

Some species of *Mobula* show strong sexual heterodonty (Herman et al., 2000, Adnet et al., 2012), with a crenulated ridge or small cusps on the lingual edge of the tooth crown of males. These crenulations strongly resemble the state observed in a small number of teeth of *Burnhamia daviesi*. It is therefore likely that *Burnhamia daviesi* exhibited sexual heterodonty, with the crenulated teeth presumably helping grip during mating. The rarity of these teeth suggests that they were not present in all males, and were probably restricted to certain parts of the jaw or only in mature males, possibly with tooth morphology changing in the breeding season, as in *Dasyatis sabina* (Kajiura and Tricas, 1996).

The genus *Burnhamia* is widespread in rocks of Eocene age, and many of the occurrences have been attributed to *Burnhamia daviesi*. Despite this, some of the

figured specimens appear to represent other species with a lower crown and more homodont dentition, as seen in *Burnhamia fetahi* Cappetta 1985. The low, narrow tooth morphology of *Burnhamia fetahi* (see Noubhani and Cappetta, 1992) appear to be restricted to the Early Eocene; teeth of Late Eocene *Burnhamia*, such as the Priabonian species of Egypt (Underwood et al., 2011) are wider and higher, more reminiscent of *Burnhamia daviesi*, as well as later genera such as *Eoplinthicus* and *Plinthicus* (see Adnet et al., 2012).

Family uncertain

*SULCIDENS* gen. nov.

(Fig. 5A–L)

**Type Species**—*Myliobatis sulcidens* Darteville and Casier, 1943

**Amended Diagnosis**—Myliobatid known only from articulated and disarticulated dentitions. Little dignathic heterodonty with teeth presumed from lower dentitions higher and more robust. Dentition of alternating rows comprising a large symphyseal tooth and one pair of lateral teeth in one row alternating with a row with two pairs of lateral teeth; symphyseal teeth are far wider than deep, lateral teeth are of similar size within the dentition and roughly diamond-shaped. Lateral teeth and lateral parts of symphyseal teeth strongly concave. Occlusal face of teeth finely granulose with in-life wear very reduced (relative to other myliobatids) or absent. Tooth crowns slightly displaced lingually. Root lobes with rounded bases and widely separated. Teeth weakly joined within dentition with suturing moderate to absent.

**Etymology**—From the sulcus in the tooth occlusal face. Usage of the same name for the genus and the species name of the type species follows the common usage of such binomial names in many extant organisms, including fish.

## DISCUSSION

*Sulcidens* gen. nov. represents a Paleocene to Early Eocene genus represented by one named species, probably in addition to undescribed forms. Symphyseal teeth of this genus are readily identifiable, even from broken fragments, although lateral teeth are very similar to those of “*Myliobatis*” *raouxi* and not readily separated. The root lobes are widely spaced, typically with the space between the root lobes being of a similar width to the root lobes themselves, and have a rounded base without flaring. The teeth are relatively low, and symphyseal teeth are of a similar height near the centre as towards their lateral margins. The occlusal faces of all teeth are concave to some degree, with a deep linguo-labial elongate groove in lateral teeth and the lateral ends of symphyseal teeth. Grooves of variable frequency and intensity are present on symphyseal teeth. Teeth are typically isolated and articulated dentitions are rare, suggesting that disarticulation occurs more rapidly than in the dentitions of other “myliobatids.”

Teeth of *Sulcidens* gen. nov somewhat resemble teeth of the approximately coeval “*Myliobatis*” *raouxi* Arambourg, 1952, (see Fig. 5M–O) which likewise does not show evidence of strong in-life wear (see Fig. 5M–O; this lack of wear is typical for the species). The occlusal face of “*Myliobatis*” *raouxi* differs from that of *Sulcidens* in that the transverse concavity of symphyseal teeth is weak or absent, but with the occlusal face instead having faint linguo-labially directed grooves and ridges.

As in *Sulcidens*, lateral teeth of “*Myliobatis*” *raouxi* have a linguo-labial groove. In addition, teeth of *Sulcidens* have widely spaced root lobes with a rounded basal face, unlike the root lobes with a flat basal face, and often more closely spaced, in “*M.*” *raouxi* and other coeval “*Myliobatis*.” “*Myliobatis*” *raouxi* should therefore be considered to be generically distinct from both *Sulcidens* and *Myliobatis* s.s., but a re-diagnosis is considered beyond the scope of this work.

*SULCIDENS SULCIDENS* (Darteville and Casier, 1943)

(Fig. 5 A–I)

*Myliobatis sulcidens* Darteville and Casier, 1943: 4, A–I (original description).

*Myliobatis sulcidens* Darteville and Casier, 1943: Arambourg, 1952: xxxii, 39–45.

? *Myliobatis raouxi* Arambourg, 1952: xxxii, 31–38. Lateral teeth of uncertain affinity

**Holotype**—Symphyseal tooth from the ?Paleocene of Cabinda Province, Angola.

**Amended Diagnosis**—As above and see Darteville and Casier, (1943)

**Material**—Three largely complete articulated dentitions and one symphyseal tooth.

**Description**—Articulated dentitions comprise alternating rows comprising a large symphyseal tooth and one pair of lateral teeth with one row alternating correspondingly with two adjacent rows of lateral teeth. The symphyseal tooth is 7–10 times as wide as deep, with similar height to depth in the presumed upper teeth; the presumed lower teeth are somewhat taller. The lateral extremities of the symphyseal teeth are somewhat displaced lingually. Lateral teeth are 1.5–2 times as wide as deep,



and diamond shaped in occlusal view; the lateralmost teeth have a straight lateral margin. The occlusal faces of all teeth are very finely granulose and this is rarely removed by in-life wear. The entire tooth occlusal face is concave in all teeth. In symphyseal teeth, a groove runs along the entire width of the tooth, becoming deeper at the lateral extremities where it intersects with a short linguo-labial groove. At this point, there is a stepped displacement of the lateral part of the symphyseal tooth lingually. The teeth have similar depth to height, and a crown slightly displaced labially relative to the root. Teeth have a faintly granulose occlusal surface which is weakly to strongly concave. In all teeth a groove runs laterally across the occlusal surface of the tooth; in lateral teeth and the lateral parts of symphyseal teeth a linguo-labial groove is also present. Where these grooves intersect there is a deep concavity in the tooth surface.

## DISCUSSION

Whilst *Sulcidens sulcidens* gen. nov. has been widely recorded from the North African Paleogene, articulated dentitions have not previously been noted, and these greatly aid the interpretation of the taxon. The presence of a large symphyseal tooth contrasting in size and shape from the rather uniform lateral teeth is very similar to the dentition of extant *Myliobatis*, as well as Paleogene taxa referred to as "*Myliobatis*". This contrasts to the situation in *Burnhamia* and extant *Rhinoptera*, where there is a gradation of tooth width away from the symphysis. In contrast, the tooth morphology, regarding both the root and crown, is very similar to *Sulcidens* and *Burnhamia*, differing largely in the general robustness and height of the teeth.

Teeth of this genus have generally been referred to “*Myliobatis*” *sulcidens* (Darteville and Casier, 1943; see Fig. 5A–I) although other species may be present (e.g. Fig. 4J, K). The type assemblage of “*Myliobatis*” *sulcidens* is poorly dated and one tooth (plate XI, 27) is indeterminate whilst another (Fig. 60b) appears to be a different species. Despite this, *Sulcidens sulcidens* is widely recorded from Morocco (e.g. Arambourg, 1952), where it is recorded from several levels within the Paleocene. In addition to Moroccan Paleocene occurrences of *Sulcidens sulcidens*, the genus is present, if uncommon, from the Early Ypresian. Incomplete and lateral teeth from the lowest six metres of Ypresian of the Khouribga area (DW, CJU pers. obs.) (Couche 1, Couche 0 and “Sillon 1” of Noubhani and Cappetta, 1992). Eocene specimens referred to *Sulcidens* are typically smaller and have a more pronounced concavity. One specimen of uncertain provenance (Fig. 5J, K) differs from *S. sulcidens* in possessing a moderate degree of suturing between adjacent teeth and more elongate lateral edges of the symphyseal teeth.

#### PHYLOGENY OF *BURNHAMIA* AND *SULCIDENS*

The phylogeny of extinct “myliobatids” is somewhat problematic, in large part due to the poor understanding of the generic affinities of many taxa. Claeson et al. (2010) concluded that early nominal “*Myliobatis*” species formed a paraphyletic group at the base of the crown group Myliobatidae + Rhinopteridae + Mobulidae (Fig. 6A). This analysis concluded that *Burnhamia* (as *Rhinoptera daviesi*) was close to *Rhinoptera* and considered *Brachyrhizodus* and *Igdabatis* to be relatively highly nested genera. An analysis based on dental characters by Adnet et al. (2012) included *Burnhamia* and placed it in a clade with extant mobulids, in turn being a sister group

to *Rhinoptera* (Fig. 6B). This study also concluded that the Myliobatidae are paraphyletic and, unlike Claeson et al. (2010), *Brachyrhizodus* is a sister-group of the rest of the clade. Phylogenies produced from molecular data give a consistent topology for extant Myliobatidae + [Rhinopteridae + Mobulidae] (Fig. 6C). In Aschliman et al. (2012), Naylor et al. (2012) and Bertozzi et al. (2016) *Rhinoptera* is considered a sister genus to the Mobulidae, and the Myliobatidae form a monophyletic group. Whilst the topology of molecular phylogenies is consistent, predicted timings of cladogenesis are not; Bertozzi et al. (2016) suggested a mid-Cenozoic divergence of the Rhinopteridae and Mobulidae even though this is inconsistent with the fossil record (e.g. Adnet et al. 2012).

Phylogenetic analyses of *Burnhamia* and *Sulcidens* gen. nov., along with a suite of extant Myliobatiformes (see Fig. 6D–F) were carried out using dental and skeletal characters. Phylogenies were produced with character states optimized using both ACCTRAN and DELTRAN models of character transformation, but the resultant consensus trees were virtually identical. Resultant trees place *Burnhamia* as a sister to the crown group Mobulidae (*Mobula* + *Manta*), which all form a sister clade to *Rhinoptera*. These taxa form a derived clade within a polytomy along with *Sulcidens*, *Aetobatus*, and *Myliobatis* + *Aetomylaeus*. The relative positions proposed for extant taxa is therefore very similar to that achieved by molecular analyses (Aschliman et al., 2012, Naylor et al., 2012), differing only in the lack of support for a monophyletic Myliobatidae. The relative position of *Burnhamia* is the same as that proposed by Adnet et al. (2012). The position of *Sulcidens* within a polytomy leaves the relative position of this genus as uncertain.

The phylogeny generated here is broadly consistent with the fossil record. The earliest records of batoid teeth within the clade including the Myliobatidae,

Rhinopteridae, and Mobulidae date from the latest part of the Cretaceous. The genera *Brachyrhizodus* and *Igdabatis* are known from numerous isolated teeth, but without articulated dentitions. The diversity in the size and shape of teeth suggest that both genera possessed a (superficially) *Rhinoptera*- like dental pattern with a large symphyseal tooth and progressively smaller teeth in more lateral positions. The stratigraphic provenance of “*Myliobatis*” *wurnoensis* White 1934 is debatable, specimens were recorded as coming from an exposure of Maastrichtian rocks (Claeson et al. 2010), but observations of the site by DJW suggest they are likely to have been loose material derived from Danian rocks higher up the slope. Despite this, it remains, along with teeth of “*Myliobatis*” ex. gr. *dixoni* Agassiz 1843 from the Danian of Morocco (CJU and DJW pers. obs), the earliest occurrence of a dentition with a *Myliobatis*-like arrangement of teeth. It is unclear whether these earliest “*Myliobatis*” should be placed in the Myliobatidae s.s., or regarded as stem group taxa. *Sulcidens sulcidens* and “*Myliobatis*” *raouxi* first appear within the early Paleocene. The earliest records of taxa similar to, but not congeneric with *Aetobatus* (see Underwood et al. 2011), *Rhinoptera* and *Burnhamia* are apparently synchronous at the base of the Eocene. This synchronicity is likely to be an artifact of poor preservation of sediments close to the Paleocene-Eocene boundary, with extreme condensation and hiatus development in the North African phosphorites, and abrupt sea level changes creating a hiatus in shallower water facies elsewhere. By the Priabonian, a [number of additional mobulid genera were present \(Adnet et al., 2012\)](#).

## EVOLUTION OF PLANKTIVORY IN BATOIDS

There is no evidence for planktivorous batoids in the Late Cretaceous.

*Cretamanta* is known from teeth that suggest a microphageous diet, but its affinity is unknown; histologically it has been demonstrated that *Cretamanta* was not a batoid (Enault et al., 2013). Both *Brachyrhizodus* and *Igdabatis* possessed robust and relatively high-crowned teeth with intense wear being common, indicating a predominantly durophageous diet. “*Myliobatis wurnoensis* and “*Myliobatis*” ex. gr. *dixoni* had high and very robust teeth and typically show intense wear, indicative of extreme durophagy. Within the early part of the Paleocene, these durophageous taxa coexisted with “*Myliobatis*” *raouxi* and *Sulcidens sulcidens*, wherein both taxa the teeth show little or no wear and were not obviously used for processing hard prey, perhaps not even wearing when filtering granular sediments. Near the base of the Eocene, at least two species of *Burnhamia* were present, also possessing teeth apparently unsuited to a durophageous diet. The early Paleogene therefore saw the appearance of several presumed planktivores which arose from durophageous ancestors.

The poorly resolved phylogenetic position of *Sulcidens* does not clearly which of the two evolutionary pathways suggested by phylogenetic analysis was followed by Myliobatiformes on the route to planktivory. It is possible that either loss of durophagy occurred independently on two occasions, or that durophagy was secondarily reacquired in *Rhinoptera*. If *Sulcidens* was present within a paraphyletic Myliobatidae (s.l.), it would indicate that *Sulcidens* acquired a concave occlusal face with rounded root bases independently from *Burnhamia* (Fig. 6E). In this scenario *Burnhamia* lost durophageous adaptations to the dentition after the change from *Myliobatis*-like to *Rhinoptera*-like heterodonty within the basal Rhinopteridae + Mobulidae. Alternatively *Sulcidens* could represent a sister taxon to the Rhinopteridae

+ Mobulidae (Fig. 6F). In this scenario, loss of durophagy would be a basal character for *Sulcidens* + Rhinopteridae + Mobulidae, and *Rhinoptera* would have only been able to acquire a strongly durophagous dentition by reversal of this condition.

The shift from being a benthic, suction-feeding durophage to a pelagic, ram-feeding planktivore is seen both within batoids and within the orectolobiform sharks, where the sister taxa, and presumably the ancestors of the whale shark *Rhincodon typus* are also benthic suction feeders. This move between different extremes of trophic ecology initially can appear counterintuitive, but apparently represent an evolutionary trend that has been followed on multiple occasions.

Benthic feeders that prey on relatively immobile prey, such as shelled mollusks, tend to themselves be mobile, as infaunal or attached prey will not come to them. As a result, many species of the Myliobatidae and Rhinopteridae, as well as larger orectolobiform sharks are highly mobile. Some species of *Aetobatus* and *Rhinoptera* are known to spend considerable time within surface waters (e.g. Blaylock, 1989), whilst many other species are present around oceanic islands indicating occasional trans-oceanic travel (Ajemian et al., 2012).

Time spent in the pelagic realm increases the exposure to the small, schooling organisms that live there. As an example of this, whilst most records of the diets of species of the Myliobatidae and Rhinopteridae comprise almost entirely of benthic organisms, one study of the diet of *Pteromylaeus* showed that a considerable quantity of small pelagic teleosts were consumed (Capapé 1977) indicating pelagic feeding, whilst anchovies were recorded in gut contents of *Rhinoptera bonasus* by Smith and Merriner (1985). These could however, be an artifact of the sampling methods by these authors, as many rays are known to ‘net-feed’ when captured in trawls or [trammel-nets \(MAK pers. obs.\)](#).

It is therefore likely that a benthic suction feeding batoid would be able to supplement its diet during movement in midwater by suction feeding small schooling organisms. A gradual shift towards a greater reliance on the pelagic foods would be accompanied by the loss of unnecessary tooth density and jaw trabeculae. This would also be associated with a change in the function of the cephalic lobes from one of food manipulation (Sasko et al. 2006) to improved hydrodynamics (Mulvany and Motta 2013).

Another possible avenue by which pelagic, ram-feeding planktivores could evolve from benthic suction-feeding durophages consuming interstitial meiofauna, is possibly evidenced by dietary studies of *Rhinoptera* in the Gulf of Mexico and off the Gulf coast of Florida in particular. Cownose rays off Florida consume infaunal shellfish like *Donax*, *Ensis*, and *Tagelus*, like their more robust and larger cousins in Chesapeake Bay, but the largest single component of their gut contents were small crustaceans like cumaceans, amphipods, and copepods (Collins et al., 2007; Ajemian and Powers, 2010; Bade et al., 2014). Sasko et al. (2006) observed cownose foraging on silted sandflats in Charlotte Harbor, Florida and found that cownose rays frequently excavate infaunal prey first using the pectoral fins and then using hydrodynamic jetting to fluidize the sandbed and expose benthic infauna. Within the gut contents of these rays, considerable amounts of sand and crushed shell fragments were evident (Collins et al., 2007; Ajemian et al., 2012). In all of these studies, *Rhinoptera* consumed a large proportion of infaunal micro-crustaceans, which it must separate from abrasive sediments without the presence of straining teeth or to our knowledge, some filtering apparatus of the jaws. These observations suggest that another possible route for planktivory starts from the benthos and moves up into the water column; from a meiofauna-filterer to a pelagic plankton-filterer. A transition

such as this one would require robust protection of the gill filaments from abrasive sediments as well as some means of cross-flow filtration or a sieve-like gill apparatus to strain benthic meiofauna from the sediment. The former method, cross-flow filtration, has already been evidenced in mobulids, the immediate sister taxa to *Rhinoptera* (Paig-Tran et al., 2013; Paig-Tran and Summers, 2014).

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Figure Captions. All figures page width.

FIGURE 1. Holotype specimen of *Burnhamia daviesi*, NHMUK P.1514. All scale bars 1cm. **A**, Lingual side of specimen showing articulated lower dentition. **B**, Labial side of specimen showing jaw cartilages and teeth from upper and lower dentition. **C**, Broken end of the specimen showing a cross section through the Meckel's cartilage and upper and lower teeth. **D**, Detail of the partly articulated lower dentition. **E**, Probable lower tooth exposed on the labial side of the specimen.

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FIGURE 2. Renders of CT scans of the holotype specimen of *Burnhamia daviesi* (NHMUK P.1514). All scale bars 1cm. **A–F**, Renders of the holotype specimen of *Burnhamia daviesi*. **A**, Composite image of the lingual side of specimen showing articulated lower dentition (green), disarticulated upper dentition (purple), Meckel's cartilage (teal) and palatoquadrate (blue). **B**, Composite image of the labial side of specimen showing disarticulated lower (green) and upper dentition (purple), Meckel's cartilage (teal) and palatoquadrate (blue). **C**, Original render of the lingual side of specimen parts of the matrix as more X-Ray dense than some of the teeth and jaws. **D**, Render of the broken edge of the specimen. The strongly mineralized end of the palatoquadrate demonstrates that fusion of the jaw cartilages was absent. **E**, Virtual transverse section through the palatoquadrate showing pyritised borings and some probable trabeculae (red). **F**, Virtual longitudinal section through the palatoquadrate showing pyritised borings and some probable trabeculae (red).

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FIGURE 3. Isolated teeth of *Burnhamia daviesi*. Scale bar is 10mm. All specimens from uncertain horizons from the London Clay of N.E. Sheppey, Kent. **A–C**, Large, presumably symphyseal upper tooth of *Burnhamia daviesi* in occlusal (**A**), basal (**B**) and oblique lingual (**C**) views. NHMUK PV P 73874. **D–F**, Lateral tooth of *Burnhamia daviesi* in occlusal (**D**), basal (**E**) and oblique lingual (**F**) views. NHMUK PV P 73875. **G–I**, Lateral tooth of *Burnhamia daviesi* in occlusal (**G**), basal (**H**) and oblique lingual (**I**) views. NHMUK PV P 73876. **J–L**, Cuspate, presumed adult male, tooth of *Burnhamia daviesi* in occlusal (**J**), basal (**K**) and oblique lingual (**L**) views. NHMUK PV P 73877. **M–O**, Faintly cuspate, presumed adult male, tooth of *Burnhamia daviesi* in occlusal (**M**), basal (**N**) and oblique lingual (**O**) views. NHMUK PV P 73878. **P–R**, Mid position tooth of *Burnhamia daviesi* in occlusal (**P**), basal (**Q**) and oblique lingual (**R**) views. NHMUK PV P 73879. **S–U**, Mid position or symphyseal tooth of *Burnhamia daviesi* in occlusal (**S**), basal (**T**) and oblique lingual (**U**) views. NHMUK PV P 73880.

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FIGURE 4. Renders of modern batoid dentitions. All scale bars 1cm. **A, B**, Renders of a juvenile specimen of *Rhinoptera bonasus* (Recent) from Chesapeake Bay, Western North Atlantic. **A**, Render of the underside of the head, including jaws, of a juvenile specimen of *Rhinoptera bonasus*. **B**, Virtual transverse section through the palatoquadrate and Meckel's cartilage of a juvenile specimen of *Rhinoptera bonasus*. **C**, Virtual transverse section through the palatoquadrate and Meckel's cartilage of a specimen of *Myliobatis* Sp. (Recent) from off Montevideo, Western South Atlantic. It is unclear from capture data whether this represents *Myliobatis goodei* or *M. freminvillei*.



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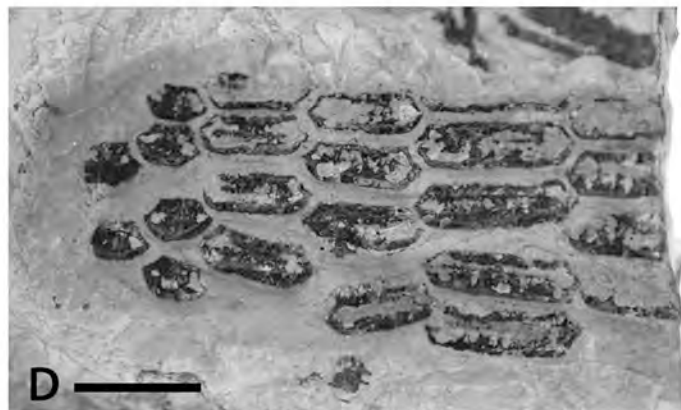
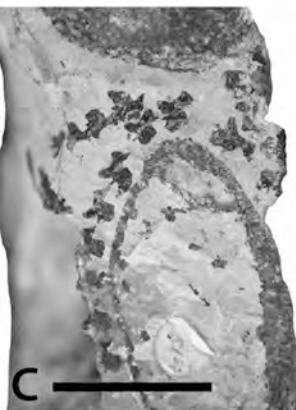
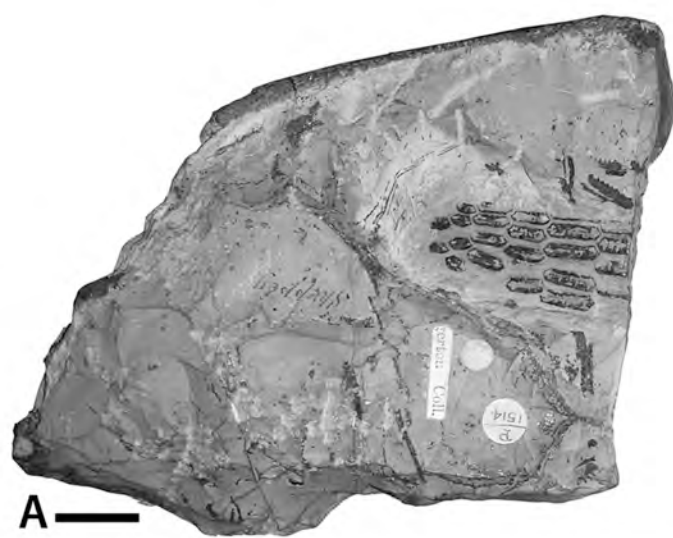
FIGURE 5. *Sulcidens sulcidens* and related taxa. Scale bar is 10mm. All specimens from uncertain sites and horizons near Oued Zem, Morocco. **A, B**, Articulated dentition of *Sulcidens sulcidens* in occlusal (**A**) and basal (**B**) views. NHMUK PV P 73881. **C, D**. Very large but incomplete upper symphyseal tooth of *Sulcidens sulcidens* in occlusal (**C**) and lateral (**D**) views. NHMUK PV P 73882. **E–G**, Articulated ?lower dentition of *Sulcidens sulcidens* in occlusal (**E**), lateral (**F**) and basal (**G**) views. NHMUK PV P 73883. **H, I**, Articulated dentition of *Sulcidens sulcidens* in occlusal (**H**) and basal (**I**) views. NHMUK PV P 73884. **J–L**, Articulated symphyseal teeth of *Sulcidens* sp. in occlusal (**J**), basal (**K**) and lateral (**L**) views. Note the suturing between teeth not seen on other specimens. NHMUK PV P 73885. **M–O**, Symphyseal tooth of “*Myliobatis*” *raouxi* in occlusal (**M**), lateral (**N**) and basal (**O**) views. Note the corrugated occlusal surface and the slight basal flaring of the root lobes. NHMUK PV P 73886.

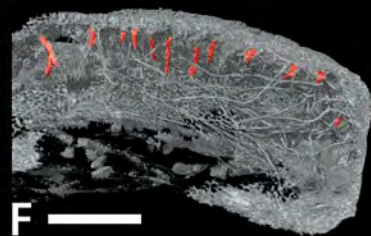
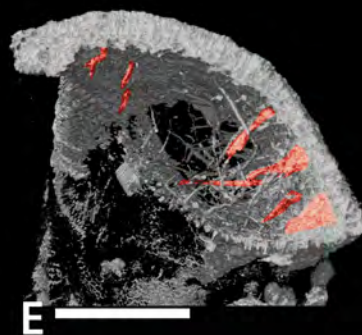
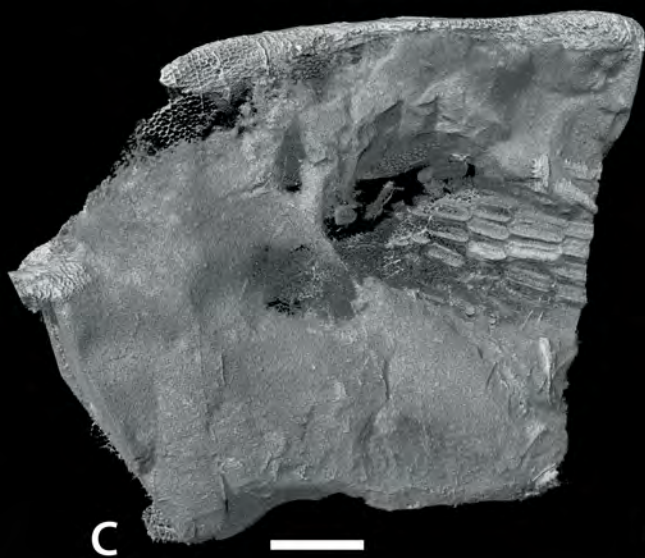
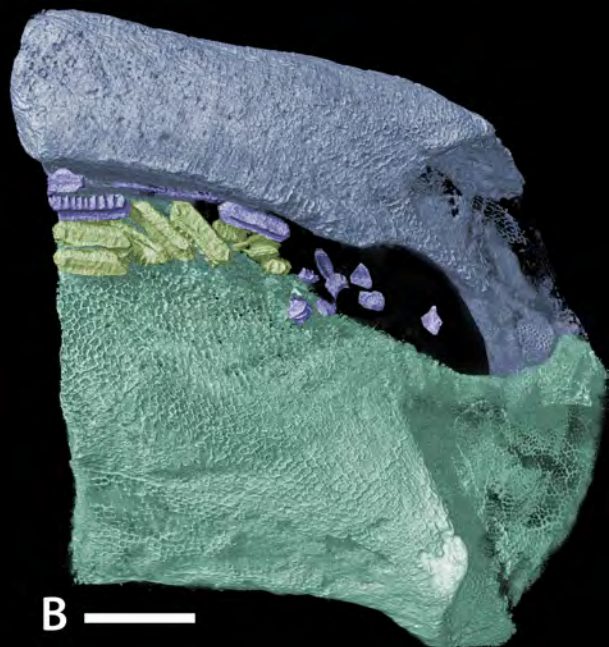
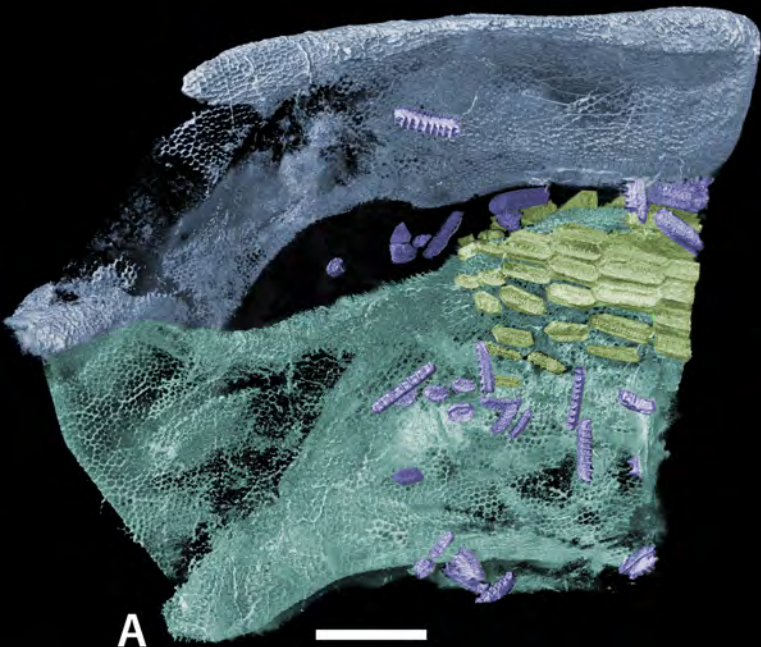
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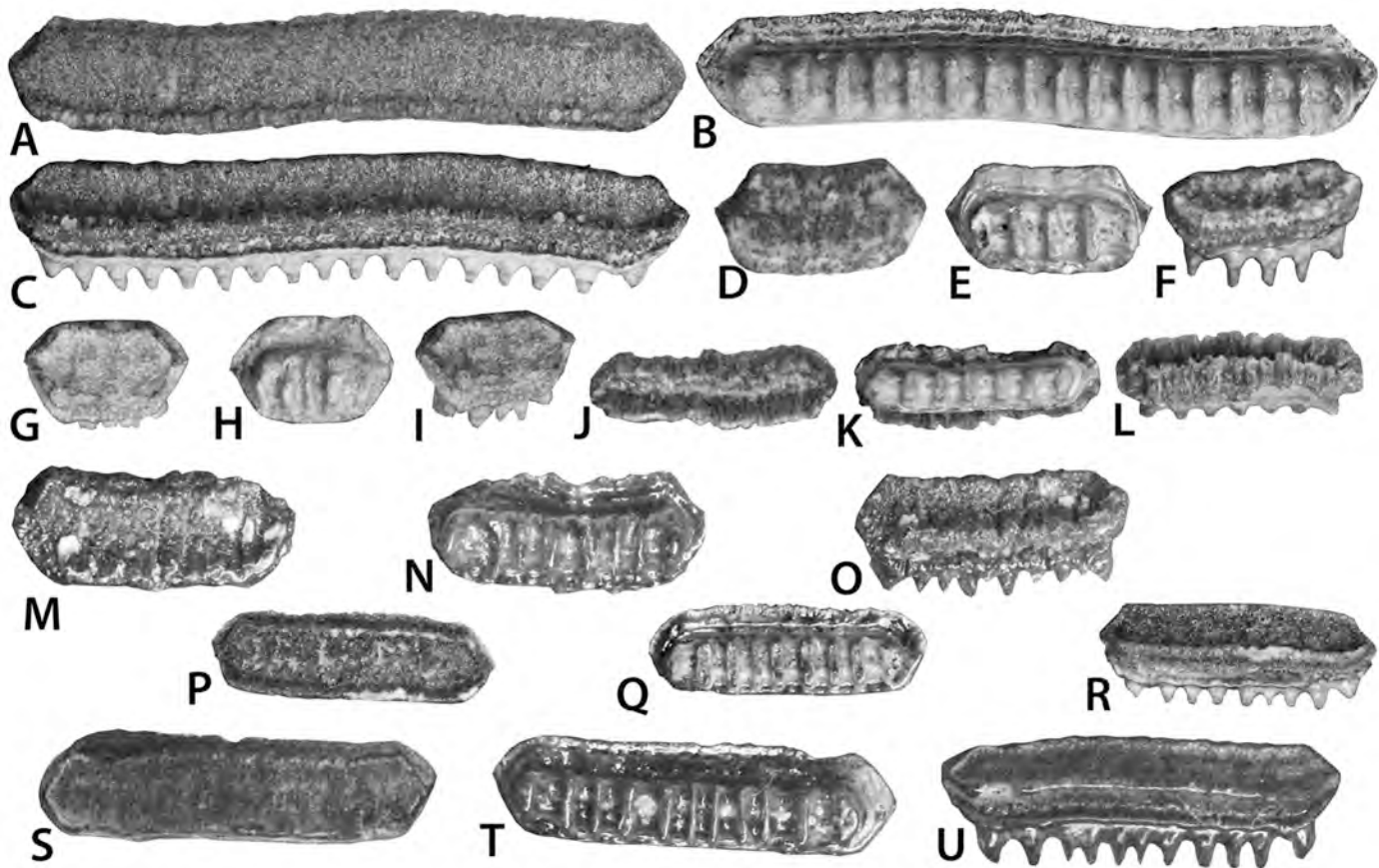
FIGURE 6. Phylogenetic position of derived Myliobatiformes including *Sulcidens* and *Burnhamia*. **A**, Phylogeny after Claeson et al. (2010) based on fossil and extant taxa, *Burnhamia* was included as *Rhinoptera daviesi* whilst some taxa included are known only from isolated teeth (*Igdabatis*, *Brachyrhizodus*). **B**, Phylogeny after Adnet et al. (2012) based on dental characters. A number of fossil mobulid taxa are not shown here. **C**, Phylogeny after Naylor et al. (2012) based on molecular data from extant taxa. The phylogeny of Aschliman et al. (2012) contains less taxa and has the

same topology for the taxa included. **D**, Bootstrapped, most parsimonious strict consensus tree using ACCTRAN transition settings (DELTRAN tree is similar with slightly lower bootstrap support for some clades). **E–F**, Possible evolutionary models for planktivory. Key relates to both diagrams. **E**, Evolutionary model for planktivory with independent loss of durophagy within *Sulcidens* and *Burnhamia*-Mobulidae. Points 1-5 refer to earliest fossil record of each clade; for point 5 see Adnet et al. (2012). Color coding identifies known durophage taxa, known planktivorous taxa and probable planktivorous taxa. Point A indicates loss of durophageous function of dentitions. **F**, Possible evolutionary model for planktivory with secondary acquisition of durophagy within *Rhinoptera*. Key as above, with Point B indicating secondary acquisition of durophageous function of dentition.

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A

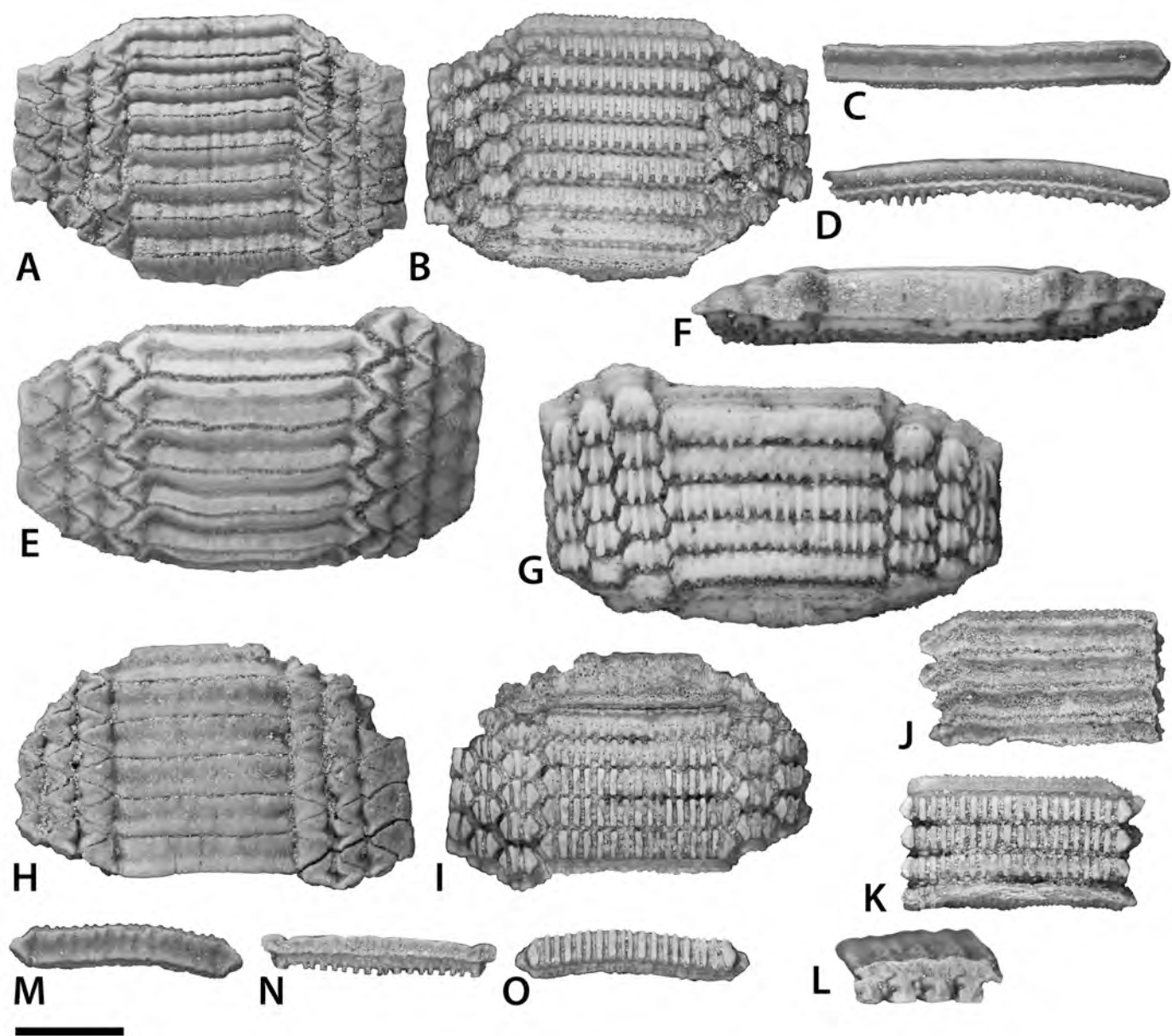


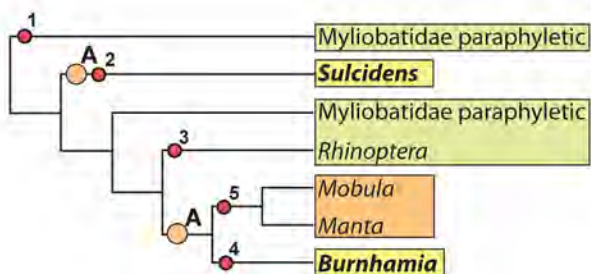
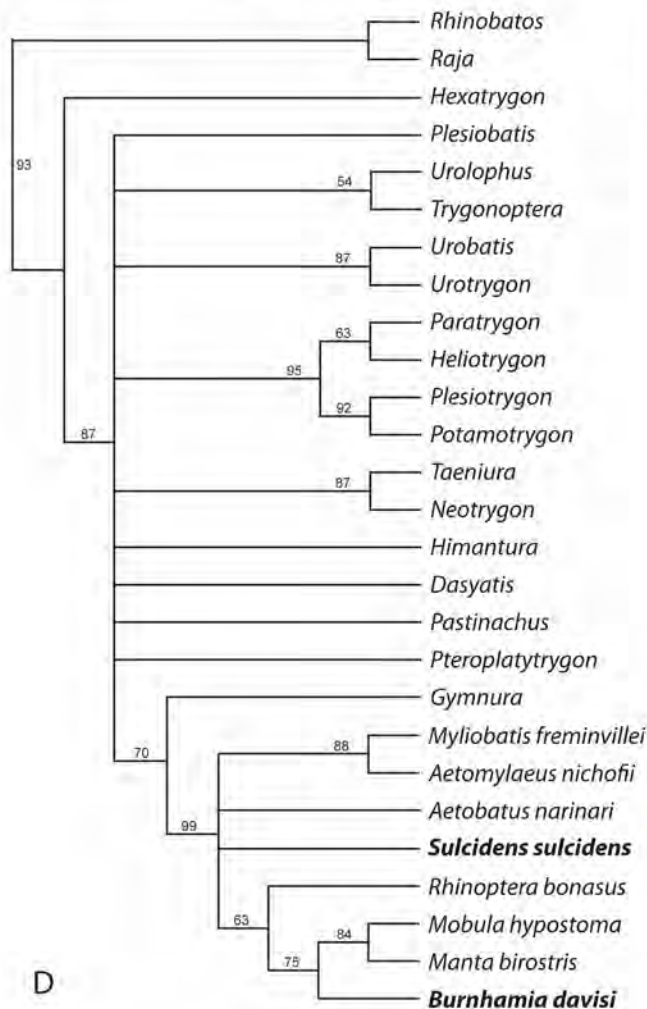
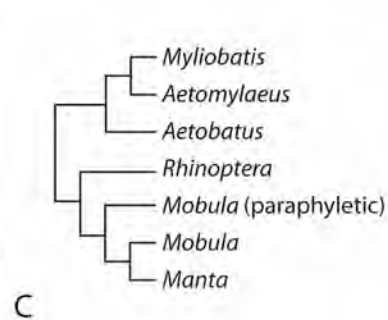
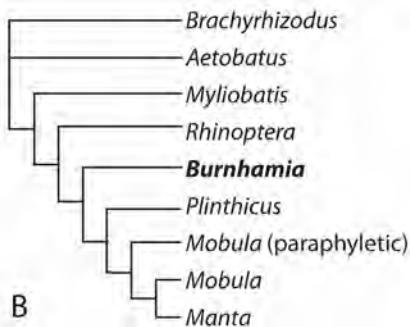
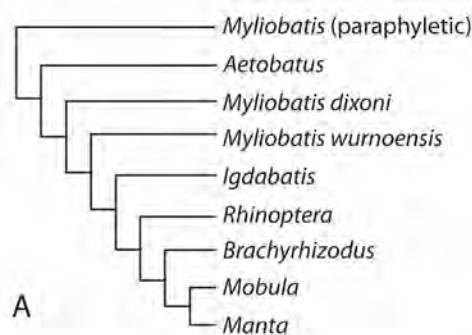
B



C





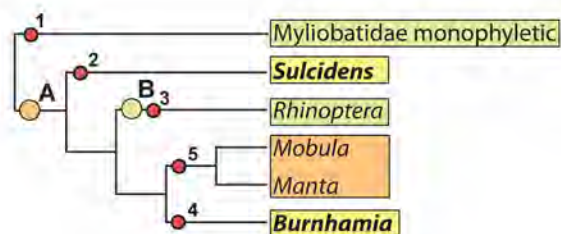


1. "Myliobatis" wurnoensis; 68-65 Ma
2. *Sulcidens sulcidens*; 65 Ma
3. *Rhinoptera* sp.; 56 Ma
4. *Burnhamia* spp.; 56 Ma
5. Several genera; 37 Ma

- Durophageous
- Probably planktivorous
- Planktivorous

**A** Loss of durophagy

**E**



**B** Secondary acquisition of durophagy



APPENDIX 1. Additional characters used in the phylogenetic analyses. All characters regarding dental and jaw morphology have either been modified from previous studies (Claeson et al., 2010; Carvalho et al., 2004; and Lovejoy, 1996).

(44) Tooth absence: (0) teeth present in both jaws; (1) teeth absent in upper jaw (*Manta*). In most batoids, the teeth are similar between upper and lower jaws, in size, shape, and generally in number (state 0). Teeth have been secondarily reduced in mobulines, with the loss of upper teeth in *Manta* (state 1).

(45) Tooth type in both upper and lower jaws: (0) non-interlocking; (1) interlocking. Most batoids have teeth with some degree of loose interdigitation, typically within the linguo-labial axis (state 0). However, the derived state includes teeth which are laterally and linguo-labially interlocking with their neighbor teeth, characteristic of in myliobatid rays (state 1).

(46) Tooth shape: (0) square to rounded; (1) hexagonal, six distinct sides; (2) rectangular with posteriorly deflected lateral margins (modified from Claeson et al., 2010). Most batoid fishes have minute, small, square to rounded teeth (in dorsal profile; state 0). In myliobatids, these teeth become hexagonal, with either equilateral sides or elongate laterally (state 1). However, as an exception among myliobatids, *Aetobatus* has a single row of laterally-expanded teeth in both the upper and lower jaws (state 2). These teeth have posteriorly deflected margins, a derived case within myliobatids.

(47) Lateral teeth: (0) present; (1) absent. One to several rows of lateral teeth exist flanking enlarged or similarly-sized symphyseal or para-symphyseal rows of teeth (state 0). These lateral

rows may be similar in size or decreasing in size medially to laterally. As stated in character [46], *Aetobatus* lacks lateral tooth rows in both the upper and lower jaws (state 1).

(48) Differentiation of medial teeth and lateral teeth (i.e. intraoral heterodonty) (modified from Claeson et al., 2010): (0) median and lateral teeth are similar (i.e. low monognathic heterodonty); (1) median teeth relatively expanded (i.e. high monognathic heterodonty). In most batoids, lateral teeth are similar in shape, size, and orientation to more symphyseally-located teeth (state 0). In some myliobatids, lateral teeth are noticeably reduced in size when compared to symphyseal or para-symphyseal rows, as in *Rhinoptera*, *Myliobatis*, and *Mobula* (state 1).

(49) Differentiation among lateral teeth: (0) lateral teeth unexpanded (i.e. disjunct heterodonty); (1) some lateral teeth expanded (i.e. gradient heterodonty). In most batoids, lateral teeth are similar in shape, size, and orientation to more symphyseally-located teeth (state 0). In some myliobatids, lateral teeth are noticeably reduced in size when compared to symphyseal or para-symphyseal rows, as in *Rhinoptera*, *Myliobatis*, and *Mobula* (state 1).

(50) Relative amount of curvature in expanded lower teeth: (0) straight and un-curved; (1) moderately curved; (2) strongly curved. From Claeson et al., 2010. The medial teeth in some extinct myliobatids might be slightly curved (state 1), while most extant species are un-curved (state 0). *Aetobatus*, however has a strongly-curved delta-shaped teeth in the lower jaw (state 2).

(51) Upper tooth curvature: (0) un-curved; (1) curved. From Claeson et al., 2010. The upper teeth in myliobatids are typically un-curved compared to the lower (state 0), the exception being *Aetobatus*. *Aetobatus*, however has a curved upper tooth plate (state 1).

(52) Sexual heterodonty : (0) Teeth of males and females the same; (1) teeth of males more cuspidate.

(53) Tooth Interlocking mechanism: (0) overlapping; (1) tongue and groove; (2) no direct contact. From Claeson et al., 2010. The manner in which anterior and posterior tooth pairs are conjoined, beyond if teeth simply overlap (state 0). In most myliobatids the teeth are interdigitated by means of a tongue and groove arrangement (state 1). The derived state, in which this interlocking pattern has been totally lost, occurs in *Mobula* and *Manta*.

(54) Shape of interlocking tongue: (0) bulbous; (1) short shelf; (2) long shelf. From Claeson et al., 2010. The morphology of the tooth-interlocking mechanism. The tongue and groove may have a posterior bulge which forms the tongue half of the mechanism, as in *Rhinoptera* (state 0). In *Myliobatis*, a short shelf interlocks with the next-most posterior tooth (state 1). In *Aetobatus*, this shelf is elongated (state 2).

(55) Vertical ridges on sides of teeth: (0) absent; (1) present. In *Myliobatis*, there are noticeable ridges of dental tissue starting at the base of the crown and extending to the occlusal surface (state 1).

(56) Suturing between occlusal surfaces of teeth : (0) absent (most); (1) occlusal joint sutured. In some species of *Myliobatis*, there is interdigitation at the boundaries between the occlusal surfaces of the teeth.

(57) Occlusal surface: (0) cusped; (1) smooth; (2) depressed. From Claeson et al., 2010. In most batoids, the occlusal surface has a low cusped crown, although in functional rows this may be worn (state 0). In myliobatids, as well as *Pastinachus*, the functional surface of the tooth is flattened (state 1). In *Manta*, the functional surface is depressed or slightly concave, *Mobula* is polymorphic for this character (state 2).

(58) Root type: (0) holaulacorrhizous; (1) polyaulacorrhizous; (2) root lobes poorly defined.

Modified from Claeson et al., 2010. Teeth have either a single root or many. In some taxa (*Burnhamia*), this definition is difficult to determine (state 2).

(59) Roots in basal view: (0) triangles; (1) wide blocks; (2) narrow blocks; (3) fine edges. From Claeson et al., 2010.

(60) Distance between roots: (0) narrower than root laminae; (1) broad, groove wider than root laminae. From Claeson et al., 2010. Most myliobatiforms have spaces between the root laminae narrower than the roots themselves (state 0). In *Rhinoptera* and *Myliobatis*, the distance between these roots is greater than the size of the roots (state 1).

(61) Inclination of roots: (0) no inclination; (1) offset and step-like; (2) long and strongly inclined.

(62) Root groove position: (0) regularly spaced between laminae; (1) irregularly spaced between laminae. The spaces between root laminae are typically regularly spaced (state 0). In other taxa (*Burnhamia*), the organization of the root complex are more haphazard (state 1).

(63) Medial symphyseal processes of the Meckel's cartilage: (0) absent; (1) presence. Some members of the genera *Himantura* and *Dasyatis* have antero-ventrally angled processes of the lower jaw, underlying the dental ligament (state 1).

(64) Lateral projections of lower jaws ("wing processes" modified from Carvalho et al 2004): (0) absent; (1) unfused; (2) fused. Absent except in the myliobatid stingrays (state 0). In most myliobatids, the wing processes are distinct bilateral processes off the Meckel's cartilage, facing posteriorly (state 1). In *Rhinoptera*, these wing processes are fused medially (state 2).

(65) Mandibular symphyses (Lovejoy 1996; Claeson et al. 2010): (0) unfused; (1) fused, tessellated partition present. In most batoids, the mandibular symphyses remain unfused and this joint maintains some degree of flexibility (state 0). In myliobatids, the mandibular symphyses are fused and akinetic (state 1).

(66). Thickening of cartilage around mandibular symphyses (Lovejoy 1996): (0) absent; (1) present. In *Burnhamia* and *Mobula*, the cartilage fusing the mandibular symphyseal surface is contiguous (state 0). For most myliobatids and *Gymnura*, there is a noticeable thickening of the cartilage on either side (bilaterally) of the symphysis (state 1).

(67) Adductor mandibulae major inserting via tendon directly into PQ (Kolmann et al. 2014): (0) absent; (1) present. For most batoids, the insertion of the primary jaw adducting muscle inserts in some manner on the upper jaw, typically by means of a thin aponeurosis into a raised process or trochanter on the palatoquadrate cartilage (state 0). In myliobatids, a substantial process on the posterior face of PQ marks the location where a large tendon inserts into the upper jaw cartilage matrix, a similar region is evident even in *Burnhamia* jaws (state 1).

(68) Lateral processes of the PQ extending far anteriorly: (0) absent; (1) present. In most batoids, there are either no lateral processes of the PQ, or only a slight enlargement (state 0). Unlike *Rhinoptera*, in *Myliobatis* and *Aetobatus*, these processes are substantial and extend far anteriorly and form as a site of muscle attachment (state 1).

(69) Anterior processes of the Meckel's cartilage: (0) absent; (1) present; (2) extending anterior past jaw joint. Some batoids lack any anterior-projecting processes off the lower jaw, like *Rhinoptera*, *Mobula*, *Raja*, and *Burnhamia* (state 0). Most batoids, in particular dasyatoids like *Trygonoptera*, *Taeniura*, and *Neotrygon*, have an obvious anteriorly-directed process (state 1).

This state is particularly exaggerated in *Dasyatis*, *Himantura*, and then in *Myliobatis* and *Aetomylaeus* (state 2).

(70) Oral gape wider than lower tooth module length: (0) equal; (1) gape width smaller; (2) gape width larger. *Rhinoptera* has a particularly wide mouth and a correspondingly laterally-enlarged tooth plates (state 0). *Aetobatus* has a particularly constrained lateral gape (state 1). Most batoids have wide gapes with the teeth extending laterally over only a small region (medial) of the overall gape (state 2).

(71) Lateral oral diastema alt: (0) diastema width greater than occlusal width; (1) occlusal width greater than diastema width. Most batoids have some form of oral diastema, a toothless space between the lateral-most extent of the dental ligament the corners of the mouth, or jaw joint (state 0). Many of the strictly piscivorous taxa, such as *Gymnura*, *Paratrygon*, and *Heliotrygon*, as well as planktivorous taxa (*Mobula* and *Manta*), have teeth extending across most of the jaw (state 1).

(72) Upper jaw profile: (0) oval in cross section (most batoids); (1) flat top, convex occlusal surface (myliobatids); (2) strongly flattened (mobulids). Most batoids have tubular-shaped jaw cartilages (state 0). The durophagous myliobatids have a more convex occlusal surface on an angular jaw (state 1). In mobulids, the jaw cartilage itself has become more plane-like, strongly flattened in an antero-posterior orientation (state 2).

(73) Upper jaw mineralization: (0) all surfaces mineralized; (1) lingual face partly unmineralized (mobulids). In most batoids, mineralized trabecular cartilage reinforces the lingual surface of the upper jaw cartilage (state 0). In *Mobula*, *Manta*, and *Burnhamia*, this upper jaw cartilage is partly unmineralized (state 1).

(74) Lower jaw profile: (0) oval in cross section; (1) strongly linguo-labially expanded. Most batoids have tubular-shaped jaw cartilages (state 0). The myliobatids as well as durophagous *Pastinachus* have a more linguo-labially expanded jaw shape (state 1).

(75) Upper jaw trabeculae: (0) absent; (1) weakly developed; (2) strongly developed. Trabecular reinforcement of the internal upper jaw cartilage is evident only in the durophagous myliobatids (state 1). Trabeculae are small and non-contiguous in *Burnhamia* and *Mobula* (state 2).

(76) Lower jaw trabeculae: (0) absent; (1) weakly developed; (2) strongly developed. Trabecular reinforcement of the internal lower jaw cartilage is evident only in the durophagous myliobatids (state 1). Trabeculae are small and non-contiguous in *Burnhamia* and *Mobula* (state 2).

(77) Lower jaw full of granular tesserae: (0) absent; (1) present. Tesserae are largely flattened within the plane of the perichondrium for most batoids (state 0). In *Mobula*, tesserae appear to be expanded and more granular, rather than flattened (state 1).

APPENDIX 2. Data matrix of characters used. Character states 1-44 follow Claeson et al., (2010).

[illegible]